DARWIN'S INFLUENCE UPON PLANT GEOGRAPHY AND ECOLOGY

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DARWIN dealt with plant geography only incidentally in connection with origin by descent. He was concerned chiefly with the bearing of migration upon community of origin, and consequently with the question of single and multiple origin of species. In his discussion of migration is found some consideration of barriers, endemism and isolation, but only in so far as these contribute to his main theme. On what might be called the ecological side proper, *i. e.*, the response of the individual, Darwin made his greatest contributions. Leaving apart his studies of pollination, movement and insectivorous plants, the ecologist must consider his fundamental work in variation and adaptation, together with his conclusions upon the questions inseparably connected with them, namely, competition, selection, inheritance of acquired characters and mutation.

In estimating Darwin's influence in all these matters, I have endeavored to keep in mind three view points: (1) his exact opinion upon each question, (2) his actual contribution to it, and (3) his share in our present knowledge of the subject, as well, perhaps, as his influence in shaping our present opinions where they do not rest on experimental knowledge. Several inherent difficulties have manifested themselves during this attempt. Chief among these is the impossibility of ascertaining what might be called the majority opinion of botanists, a difficulty aggravated by the fact that no two botanists would draw the same line between what is proved and what is merely held. In addition, Darwin's own views seem to have remained plastic to a degree not always evident in his most widely read books. This has brought the curious result that his earlier views have often had much the greater

influence in moulding opinion, while his later views are more in accord with scientific knowledge. Furthermore, it must be borne in mind that Darwin was the great apostle of origin by descent. It was his unique mission to bring the scientific world to accept this doctrine, a task of such magnitude that methods of origin, for the time at least, were relatively unimportant. In attempting to determine Darwin's actual contribution, one is confronted by the task of deciding how much credit is to be given to the discoverer of a new idea or principle, and how much to him who applies it and establishes it. It is fairly well known that Darwin was not the first to formulate the principle of evolution. Even in regard to natural selection, often accepted as distinctly Darwinian, Darwin himself has shown that he was anticipated by three other writers. Yet the fact remains that Darwin has contributed more to the foundations of biology than all of his forerunners.

A careful rereading of the "Origin of Species" and the "Variation of Animals and Plants under Domestication" has been found necessary to make Darwin's views emerge clearly from the mists of tradition and of recollection. It has seemed desirable also that he should himself speak in his own words, without the handicap of paraphrase and of the personal equation. Together with the manifest difficulty of making accurate and definite statements of the consensus of botanical opinion on mooted questions, this necessarily results in a more or less fragmentary and detached account of such a vast field.[1] Its value lies wholly in recalling to us Darwin's actual views without interpretation or emendation, so that each may determine for himself what part Darwin's work plays in his own views, and in botanical opinion as he sees it.

DISTRIBUTION

Darwin formulated three laws of distribution: (1) "Neither the similarity nor the dissimilarity of the in-

[1] The references given after the various excerpts are to the sixth edition (1872) of the "Origin of Species," and to the second edition (1875) of the "Variation of Animals and Plants under Domestication."

habitants of the various regions can be wholly accounted for by climatal or other physical conditions," (2) "barriers of any kind or obstacles to free migration, are related in a close and important manner to the differences between the productions of various regions," (3) "the affinity of the productions of the same continent, or of the same area, though the species themselves are distinct at different points and stations."[2] These scarcely need comment, for they arise clearly from the law of origin by descent. They are such an intrinsic part of the foundation of plant geography as to require an effort to recognize the fact that it was once necessary to formulate them.

Single and Multiple Origin

From the very nature of his task, Darwin was forced to assume that species were first produced at one spot. To-day the fact that the same species may arise at two or more distinct places merely strengthens the law of descent, but in Darwin's time this would have greatly increased the difficulty of supporting his doctrine by the evidence drawn from the distribution of plants. Darwin's views upon this question were far from uncertain, as the following excerpt indicates.

> It is obvious that the individuals of the same species, though now inhabitating distant and isolated regions, must have proceeded from one spot, where their parents were first produced. We are thus brought to the question which has been largely discussed by naturalists, namely, whether species have been created at one or more points of the earth's surface. Undoubtedly there are many cases of extreme difficulty in understanding how the same species could possibly have migrated from some one point to the several distant and isolated points where now found. Nevertheless, the simplicity of the view that each species was first produced within a single region captivates the mind. He who rejects it, rejects the *vera causa* of ordinary generation with subsequent migration, and calls in the agency of a miracle.[3]

This view seems to be little more than an inheritance from the special creationists. It doubtless reflects the prevailing opinion of Darwin's time, and probably is in

[2] "Origin," 2: 129.
[3] "Origin," 2: 135.

accord with the consensus of opinion at present. What the current opinion is can only be a matter of conjecture, but notwithstanding the proofs of multiple origin afforded by adaptation and mutation, it would seem that the majority of botanists and nearly all zoologists still adhere to the doctrine of single origin.

MIGRATION

Darwin's treatment of migration is limited to evidence of the possibility of distant and occasional migration as the explanation of the many puzzles of distribution. It is evident that his position in regard to single origin caused him to turn to migration as the necessary solution of all the problems of distribution. His attitude upon both questions is shown by the following statement:

> Whenever it is fully admitted, as it will some day be, that each species has proceeded from a single birthplace, and when in the course of time we know something definite about the means of distribution, we shall be enabled to speculate with security on the former extension of the land.[4]

His experiments upon the carriage of seeds and fruits by ocean currents and by birds, though necessarily crude and simple, are classic. They still serve to indicate one of the really fundamental points of attack in the detailed quantitative study of migration.

VARIATION

A brief summary of Darwin's views upon variation is an impossibility. Under the headings "Causes of Variation," "Habitat as Cause," "Use and Disuse," I have assembled his own statements to make clear his position. These seem to differ in some essentials from the views often ascribed to Darwin, or at least held by many who regard themselves as his followers. They appear to be more in accord with the views of the ecologist who looks to the habitat for the final explanation of all changes, than with the opinions held by biologists in general. They show Darwin to have been much more in sympathy with

[4] "Origin," 2: 140.

Lamarck and Saint-Hilaire than he was himself aware. He thus becomes the connecting link between these two great but less appreciated seers, and the investigators of to-morrow whose success will rest on the experimental study of the habitat as the primary cause.

Causes of Variation.

I have hitherto sometimes spoken as if the variations so common and multiform with organic beings under domestication, and in a lesser degree under nature—were due to chance. This, of course, is a wholly incorrect expression, but it serves to acknowledge plainly our ignorance of the cause of each particular variation.[5]

No doubt each variation must have its efficient cause, but it is as hopeless to discover the cause of each as it is to say why a chill or a poison affects one man differently from another. Even with the modifications resulting from the definite action of the conditions of life, when all or nearly all the individuals which have been similarly exposed, are similarly affected, we can rarely see the precise relation between cause and effect.[6]

We must . . . conclude that organic beings, when subjected during several generations to any change whatever in their conditions, tend to vary: the kind of variation which ensues depending in most cases in a far higher degree on the nature or constitution of the being, than on the nature of the changed conditions.[7]

Those authors that adopt the latter view—that variability must be looked at as an ultimate fact, would probably deny that each separate variation has its own exciting cause. Although we can seldom trace the precise relation between cause and effect, yet the considerations presently to be given lead to the conclusion that each modification must have its own distinct cause, and is not the result of what we blindly call accident.[8]

Habitat as Cause.

With respect to what I have called the indirect action of changed conditions, namely, through the reproductive system being affected, we may infer that variability is thus induced, partly from the fact of this system being extremely sensitive to any change in the conditions. Many facts clearly show how eminently susceptible the reproductive system is to very slight changes in the surrounding conditions.[9]

Changed conditions of life are of the highest importance in causing variability, both by acting directly upon the organization, and indirectly by affecting the reproductive system. It is not probable that variability is an inherent and necessary contingent under all circumstances.[10]

[5] "Origin," 1: 164. [6] "Variation," 2: 273.
[7] "Variation," 2: 229. [8] "Variation," 2: 232. [9] "Origin," 1: 10.

These several conditions alone render it probable that variability of every kind is directly or indirectly caused by changed conditions of life. Or, to put the case under another point of view, if it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability.[11]

We have good reason to believe, as shown in the first chapter, that changes in the conditions of life give a tendency to increased variability, and in the foregoing cases the conditions have changed, and this would manifestly be favorable to natural selection, by affording a better chance of the occurrence of profitable variations.[12]

Use and Disuse.

It is notorious, and we shall immediately adduce proofs, that increased use or action strengthens muscles, glands, sense-organs, etc., and that disuse, on the other hand, weakens them.[13]

There can be no doubt that with our anciently domesticated animals, certain bones have increased or decreased in size and weight owing to increased or decreased use. With animals living a free life and occasionally exposed to severe competition, the reduction would tend to be greater, as it would be an advantage to them to have the development of every superfluous part saved.[14]

COMPETITION

In spite of the importance Darwin assigned to competition, for to him it usually comprises the whole process of natural selection, he gave little thought to its analysis and almost none to its investigation. His ideas of competition were drawn largely from Lyell and Herbert, and he was content to take it as a universal and fundamental process among living things, without detailed inquiry into its working or its precise relation to the origin of new forms. Darwin's actual contribution rests chiefly upon his formulation of the following law of competition, which recent quantitative experiments indicate to be fundamental:

As species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them if they come into competition with each other, than between the species of distinct genera.[15]

[10] "Origin," 1: 49.
[11] "Variation," 2: 234.
[12] "Origin," 1: 100.
[13] "Variation," 2: 276.
[14] "Variation," 2: 280.

Competition has, however, been almost completely neglected until the ecologist has begun the investigation of it in the last few years, and there are few subjects in which botanical opinion is so completely unformed.

Inheritance of Acquired Characters

Darwin's opinions upon this subject appear to have been modified little with time, contrary to the case with other views. Here again he was in almost complete accord with Lamarck and Saint-Hilaire, but he seems to have had little effect upon current opinion, especially among zoologists. The experimental ecologist would doubtless follow Darwin in regarding the inheritance of acquired characters as proved beyond question. Indications are not lacking that more and more botanists are coming to the same point of view. Darwin's attitude may be summed up in the following:

The increased use and disuse of various organs produces an inherited effect.[16]

With plants, the period of vegetation is easily changed, and is inherited, as in the case of summer and winter wheat, barley and vetches.[17]

Changed habits produce an inherited effect, as in the period of the flowering of plants when transplanted from one climate to another.[18]

Habit is hereditary with plants, as in the period of flowering, in the time of sleep, in the amount of rain requisite for seeds to germinate, etc.[19]

Perhaps the correct way of viewing the whole subject would be to look at the inheritance of every character whatever as the rule, and non-inheritance the anomaly.[20]

Mutation

Darwin's attitude towards the sudden appearance of striking variations, of sports, and monstrosities towards what is now called mutation, is one held by the majority of American botanists to-day. To the latter, DeVries has supplied the scientific proof of origin by sudden and striking variation, but only a small number, the followers of DeVries, regard mutation as the fundamental or uni-

[15] "Origin," 1: 93.
[16] "Variation," 2: 273.
[17] "Variation," 2: 285.
[18] "Origin," 1: 12.
[19] "Origin," 1: 173.
[20] "Origin," 1: 15.

versal process. Zoologists, it would seem, incline to look with greater favor upon mutation as the regular method of origin.

At long intervals of time, out of millions of individuals reared in the same country and fed on nearly the same food deviations of structure, so strongly pronounced as to deserve to be called monstrosities, arise; but monstrosities cannot be separated by any distinct line from slighter variations. All such changes of structure, whether extremely slight or strongly marked, which appear amongst many individuals living together, may be considered as the indefinite effects of the conditions of life on each individual organism.[21]

Some naturalists have maintained that all variations are connected with the act of sexual reproduction, but this is certainly an error: for I have given in another work a long list of "sporting plants," plants which have suddenly produced a single bud with a new and sometimes widely different character.[22]

Some variations useful to man have probably arisen suddenly, or by one step.[23]

No one supposes that our choicest productions have been produced by a single variation from one stock.[24]

It may be doubted whether sudden and considerable deviations of structure such as are occasionally seen in our domestic productions, more especially with plants, are ever permanently propagated in a state of nature.[25]

I saw also that the preservation in a state of nature of any occasional deviation of structure, such as a monstrosity, would be a rare event, and that if first preserved, it would generally be lost by subsequent intercrossing with ordinary individuals.[26]

ADAPTATION

Darwin recognized the three fundamental methods of origin in nature, namely, variation, mutation and adaptation. It seems probable that to mutation he assigned its approximate value. In the "Origin of Species," variation with selection was given the preeminent place, and adaptation a minor one. Later, adaptation assumed greater importance to his mind, and there is some evidence that he may have assigned to it a value greater than that of variation. He had come to see more clearly that natural selection operated upon things already produced,

[21] "Origin," 1: 9.
[22] "Origin," 1: 11.
[23] "Origin," 1: 34.
[24] "Origin," 1: 37.
[25] "Origin," 1: 52.
[26] "Origin," 1: 111.

and to catch a glimpse of the fact that indefinite action, *i. e.*, variation, and definite action of the habitat, *i. e.*, adaptation, were at bottom the same thing.

His changing view point is recorded in his letters, and hence his later views are not generally known. As a result, scientific opinion has been more or less stereotyped in the well-known statements of the "Origin of Species" and has maintained in greater or less degree a position which Darwin himself had forsaken. Darwin's later opinions upon adaptation, as upon the causes of variation, and upon the inheritance of acquired characters, did not differ essentially from those of Lamarck. More important than this, for Lamarck was a prophet, not an investigator, they are in accord with the first results of the application of exact ecological methods to the question of the origin of new forms in natural habitats.

As far as I am able to judge, after long attending to the subject, the conditions of life appear to act in two ways—directly on the whole organization or on certain parts alone, and indirectly by affecting the reproductive system.[27]

In looking at many small points of differences between species, which, as far as our ignorance permits us to judge, seem quite unimportant, we must not forget that climate, food, etc., have no doubt produced some direct effect.[28]

In all cases, there are two factors, the nature of the organism, which is much the most important of the two, and the nature of the conditions. The direct action of changed conditions leads to definite or indefinite results. In the latter case, the organization seems to become plastic and we have much fluctuating variability. In the former case, the nature of the organism is such that it yields readily when subjected to certain conditions, and all or nearly all the individuals become modified in the same way. It is very difficult to decide how far changed conditions, such as climate, food, etc., have acted in a definite manner. There is reason to believe that in the course of time the effects have been greater than can be proved by clear evidence.[29]

The greatest mistake I made was, I now think, I did not attach sufficient weight to the direct influence of food, climate, etc., quite independently of natural selection. When I wrote my book, and for some years later, I could not find good proof of the direct action (*i. e.*, in producing definite variations) of the environment upon the species. Such proofs are now plentiful.[30]

[27] "Origin," 1: 8.
[28] "Origin," 1: 104.
[29] "Origin," 1: 165.
[30] "Life and Letters," 3: 159, 1876.